Overeating, Dietary Selection Patterns and Sucrose Intake in Growing Rats[1]

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HIRSCH, E., C. DUBOSE AND H. L. JACOBS. *Overeating, dietary selection patterns and sucrose intake in growing rats.* PHYSIOL. BEHAV. 28(5) 819–828, 1982.—Weanling rats were allowed access to food for either 5 hours or 24 hours per day. Within each food availability condition one group had access to a complete diet and one group had access to the complete diet and a 32% solution of sucrose. Caloric intake and rates of growth were considerably higher in the 24 hour access groups. The availability of sucrose led to a small (10–15%) but consistent elevation in caloric intake in the ad lib condition but did not influence growth in either food availability condition. Absolute levels of sucrose intake and the proportion of calories taken from the sucrose solution were consistently higher in the ad lib group and increased with increases in body size for both groups. Dilution of the chow component or the sucrose component of the diet did not alter dietary selection patterns in either food availability condition. It appears that access to a palatable carbohydrate solution can lead to overeating in the rat but these solutions do not induce the rat to select imbalanced diets that compromise growth.

Caloric intake   Dietary selection   Overeating   Growth   Sucrose intake

THE role of the sensory properties of food on energy intake and dietary selection patterns remains problematic. Adolph's [1] classic experiments clearly argued for the primacy of caloric factors in the control of energy intake. This view has been supported by experiments that either minimize orosensory stimulation [31, 44, 46] or find that the daily level of energy intake is largely unaffected by changes in the smell, taste, or texture of the available food source [7, 13, 18, 27, 42]. This body of work has led to widespread acceptance of the assertion that rats normally eat for calories and that the sensory properties of food have only a minor influence on the daily level of intake. Richter [33] has taken this position to its extreme in stating that "It is almost impossible to force a normal rat to eat more than its fixed limit of calories" (p. 396).

In a similar manner the ability of rats to self select an optimal diet from a variety of food sources has largely been attributed to the nutritional consequences of ingestion despite the fact that the underlying mechanism for this process remains unspecified [2, 22, 32]. When sensory factors are considered in relation to dietary self selection they are usually invoked to explain failures of regulation when poor tasting protein sources are employed [22]. A potentially important role for sensory factors, as conditioned stimuli that mediate self selction, has been suggested but remains largely unexplored [37,38].

In contrast to a view which emphasizes the over-riding roles of caloric control and dietary balance as determinants of feeding behavior there is a growing body of evidence which shows that changes in the nutritional and sensory properties of the available diet can lead to overeating and obesity in laboratory animals. There are at least three types of dietary regimens that produce these effects. Ingle [16] first reported that obesity could be produced in rats by restraining their movement and offering them a calorically dense, appetizing diet. Subsequently many investigators have shown that high fat diets, without activity restriction, lead to overeating and obesity in rats [3, 23, 26, 39] and mice [10,11]. A second type of dietary procedure which leads to obesity was first reported by Sclafani and Springer [41]. When rats are allowed access to a complete diet and a supermarket array of palatable foods, overeating, rapid weight gain and excess fat deposition are observed [34, 35, 36, 41]. The third type of dietary regimen that leads to obesity in rats provides the experimental animals with a nutritionally complete diet and a separate carbohydrate source. Solutions of sucrose [9, 19, 28], as well as granular sucrose [21], are effective in promoting excess energy intake under these conditions. These observations make it abundantly clear that the nature of the available diet can lead the rat to ingest excess calories. However, the features of these diets that promote excess intake remain to be specified in an adequate manner.

Of the three dietary regimens that have been employed to produce overeating and obesity the procedure that appears

to hold the most promise as an analytic tool for identifying the factors that induce hyperphagia in these otherwise normal animals involves offering a nutritionally complete diet and a separate carbohydrate source. In contrast to both the supermarket diet and the high fat diet this form of high carbohydrate diet allows specification of the sensory and nutritional properties of the diet and their independent manipulation.

In an attempt to specify the determinants of carbohydrate-induced overeating the present experiment examines the influence of deprivation and nutrient dilution on caloric intake and dietary selection when growing rats are given access to either a complete diet (Purina chow) or the complete diet and a sapid carbohydrate solution (32% sucrose). Two groups of growing rats had ad lib access to one of these diets and a second two groups had access to one of these diets for only five hours per day.

Interest in the growing rat in this experiment stems from two sources. With a complete diet and a sucrose solution freely available young rats overeat, deposit excess fat, but do not gain weight faster than chow fed controls [20,28]. The growth curves presented by Muto and Miyahara [28] suggest that the sucrose fed animals were beginning to gain weight faster than the controls at about 70 days of age. One purpose of the present experiment is to extend the period of observation in order to define the age where excess caloric intake leads to an elevation in body weight. A second reason for studying the growing rat concerns the well documented decline in the rat's protein requirement with age [14,24]. By monitoring changes in dietary selection with age it is possible to test the hypothesis that the intake of sweet carbohydrate solutions is controlled on a long-term basis by the animal's total nutritive requirements [6,8]. This view leads to the prediction that relative sucrose intake (proportion of calories taken from sucrose) will increase with age.

The five-hour restriction on food availability was introduced to make the testing conditions more demanding and to examine the effects of food deprivation on intake and preference for the two dietary components. Both intake and preference for sweet solutions are markedly increased by food deprivation [6, 18, 47]. The question of interest in the present experiment is whether the effects of deprivation are sufficiently powerful to induce these animals to consume too much of the sweet solution at the expense of the essential nutrients (protein, vitamins and minerals) contained in the complete diet. With access to a low protein diet (9%) and a sugar solution, growing rats show poor selection and growth is impeded relative to a control group fed only the low protein diet [28]. On the basis of this observation one would predict poor selection and growth in the sucrose group restricted to five hours of access to food per day. Alternatively a view of sucrose intake which emphasizes the controlling nature of the animal's total nutritive requirements would predict similar growth in both restricted groups [7,8]. A further test of this hypothesis is provided in the present experiment by examining the effect of diluting both sources on caloric intake and dietary selection. In the last phase of this experiment the restriction on food availability was removed to determine how a prolonged period of restricted intake and slower growth would influence intake and recovery growth.

METHOD

Animals

Twenty eight, male, Sprague-Dawley (Madison, WI) rats

were used. The animals were 21 days of age at the beginning of testing. They were assigned to one of four groups that were matched on the basis of body weight.

Apparatus

The animals were housed individually in wire mesh cages (25×18×18 cm, Wahmann Manufacturing Co., Baltimore, MD) in a room that was on a 12:12, light-dark cycle with the lights coming on at 0800 hours. Purina chow (3.61 kcal/g) was available in 5 cm diameter cups with lids that had 4.45 cm diameter openings in the center. The cups were held in place in the rear corner of the cage with an upright bolt. Food spillage was negligible under these conditions. Water was continuously available in 100 ml calibrated bottles. Sucrose was available in 250 ml calibrated bottles. The bottles were mounted on the front of the cages with the drinking spouts approximately 2 cm above the floor and 3 cm apart. The positions of the sucrose and the water bottles were alternated daily. The sucrose solution was prepared from commercial sugar and tap water 24 hours prior to use on a weight per volume basis.

Procedure

The experiment was conducted in four phases. During phase 1, two groups had 24 hours access to food and water. The other two groups had five hours of access to food and the sucrose solution, and 24 hours of access to water. Within each food availability condition (5 hr or 24 hr) one group was offered Purina chow (P) and the second group was offered Purina chow and a 32% sucrose solution (PS). The five hour period of food availability began at 0800. Measurements of food intake, water intake and body weight were taken daily. Phase 1 lasted 44 days.

During the first five days of phase 2 the Purina chow was diluted 25% by the addition of kaolin. This was followed by a six day period of access to the unadulterated chow before phase 3 was initiated. Throughout phase 2 the 32% sucrose solution remained available for groups 5PS and 24PS. During phase 3 the sucrose solution was diluted 50% by the addition of water for these two groups. The resulting 16% sucrose solution was available for the first six days of phase 3. This was followed by a five day period of access to the 32% solution before phase 4 was initiated. During phase 4 the two five-hour groups were allowed 24 hours access to Purina chow or to Purina chow and sucrose for an additional 24 days.

Data Analysis

The data from phases 1 and 4 were analyzed by a three way analysis of variance with access time (5 hr or 24 hr) and diet (P or PS) as between groups factors and days as a repeated measures factor. The data from phase 2 were also analyzed by a three way analysis of variance with access time and diet as between groups factors and dilution (diluted or undiluted chow) as a within group factor. The data for the two dilution conditions were collapsed across days. The data for phase 3 were analyzed with a two way analysis of variance with access time as a between groups factor and concentration (16% or 32%) as a within groups factor. The data for each concentration were collapsed across days. All differences discussed are significant at least at the 5% level.
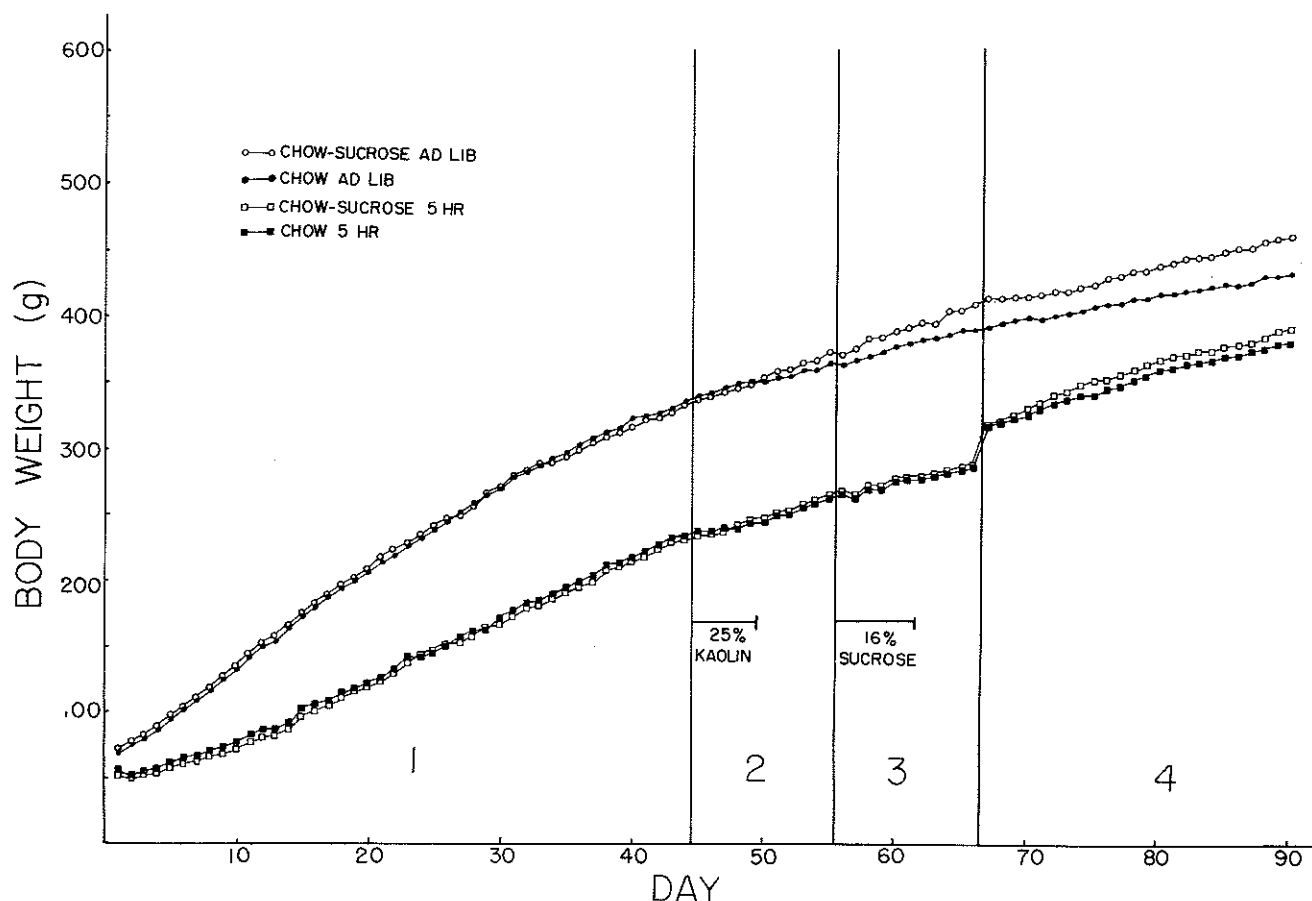
FIG. 1. Mean body weight in rats fed a complete diet or a complete diet plus a 32% sucrose solution for 5 hours or 24 hours each day.

RESULTS

Figure 1 shows that access time had a pronounced effect on body weight and the rate of weight gain. Throughout the first three phases of this experiment the animals with ad lib access to food weighed more and gained weight faster than the 5 hr groups. Access to sucrose did not have any effect on body weight in either food availability condition, although in the last phase of the experiment the groups with ad lib access to sucrose and chow appeared to gain weight faster than the two chow only groups. This apparent difference in the rate of weight gain during phase 4 was not statistically significant. Similarly the small difference in body weight (34 g) on the final day of the experiment between groups 24PS and 24P was not statistically significant. During phase 4, when the 5 hr groups were allowed unrestricted access to food, both formerly restricted groups showed an immediate spurt in growth. On the first day of ad lib access to food both groups gained 30 g. During the remainder of phase 4 these two groups continued to gain weight at a faster rate than the two groups that had been allowed ad lib access to food throughout the experiment. Figure 1 also suggests that these groups would have attained the control level of body weight if this phase of the experiment had lasted longer.

Total caloric intake is shown in Fig. 2. During phase 1 caloric intake was substantially higher in the 24 hr access condition. The availability of sucrose led to a small (10–15%) but highly significant elevation in daily caloric intake in the

ad lib condition. Access to sucrose did not have any effect on daily caloric intake in the 5 hr condition. Under both conditions of food availability caloric intake increased as growth progressed. The increase in caloric intake with changes in body size showed a somewhat different pattern in the two conditions of food availability. The ad lib groups showed a sharper initial rate of increase that asymptoted after approximately 25 days, at around 100 kcal per day. The restricted animals showed a much more gradual pattern of increase that lasted throughout phase 1.

During phase 2, kaolin dilution led to a small but significant decrease in caloric intake for all groups. The average caloric intake during each part of phase 2 is shown in Table 1. The animals with ad lib access to food showed a more complete compensatory response to the kaolin dilution than the 5 hr animals. During the period of kaolin dilution the ad lib animals showed a 6% reduction in daily caloric intake whereas the 5 hr animals showed an 18.5% decrease. The availability of sucrose did not influence caloric adjustment when the chow component of the diet was diluted.

During phase 3 there was no change in caloric intake when the sucrose solution was diluted 50%. There was a tendency for both groups to consume a few more calories per day when the 32% solution was offered, but this effect was not statistically significant.

During phase 4 the formerly restricted groups showed a large increase in caloric intake. This increase was more
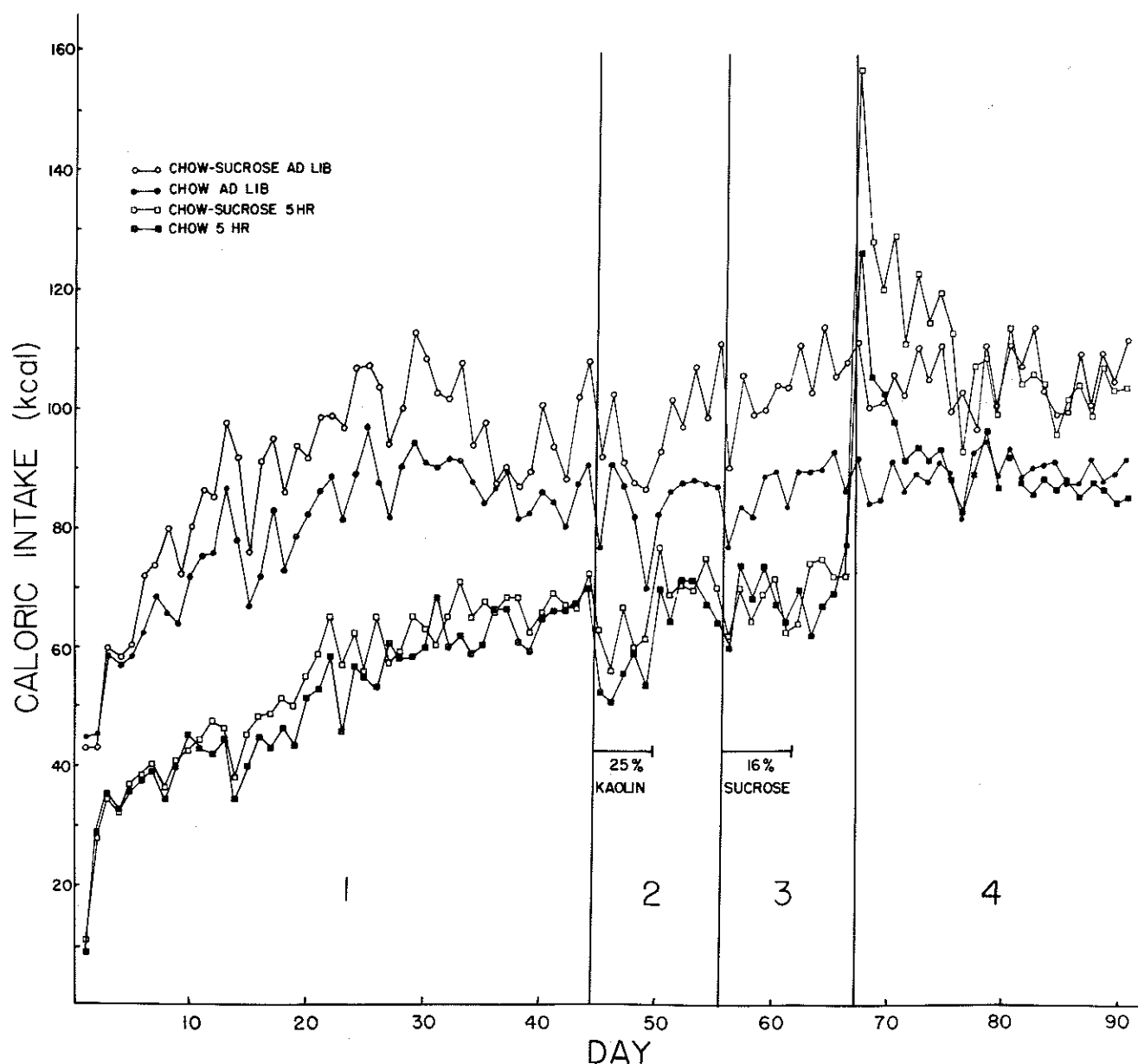
FIG. 2. Mean daily caloric intake in rats fed a complete diet or a complete diet plus a 32% sucrose solution for 5 hours or 24 hours each day.

TABLE 1

CALORIC INTAKE DURING DIET DILUTION

Group	Kaolin Dilution Caloric Intake (kcal ±S.D.)	No Dilution Caloric Intake (kcal ±S.D.)	% of Undiluted Intake
5PS	61.5 ± 8.05	72.4 ± 9.40	84.9
5P	55.1 ± 8.21	69.1 ± 7.80	79.7
24PS	92.3 ± 10.40	100.1 ± 12.60	92.3
24P	81.5 ± 9.41	86.5 ± 11.82	94.2

pronounced and lasted longer for the group with access to sucrose. However, within ten days both groups showed levels of daily caloric intakes that were indistinguishable from the groups that had been allowed ad lib access to food throughout the experiment. During phase 4 both sucrose groups had significantly higher levels of caloric intake than both chow groups.

Figure 3 shows chow intake during the course of the experiment. During phase 1 the effects of access time and diet were highly significant and these variables interacted with each other as well as with days. The three way interaction between access time, diet and days was also highly significant. This pattern of results can be interpreted in the follow-
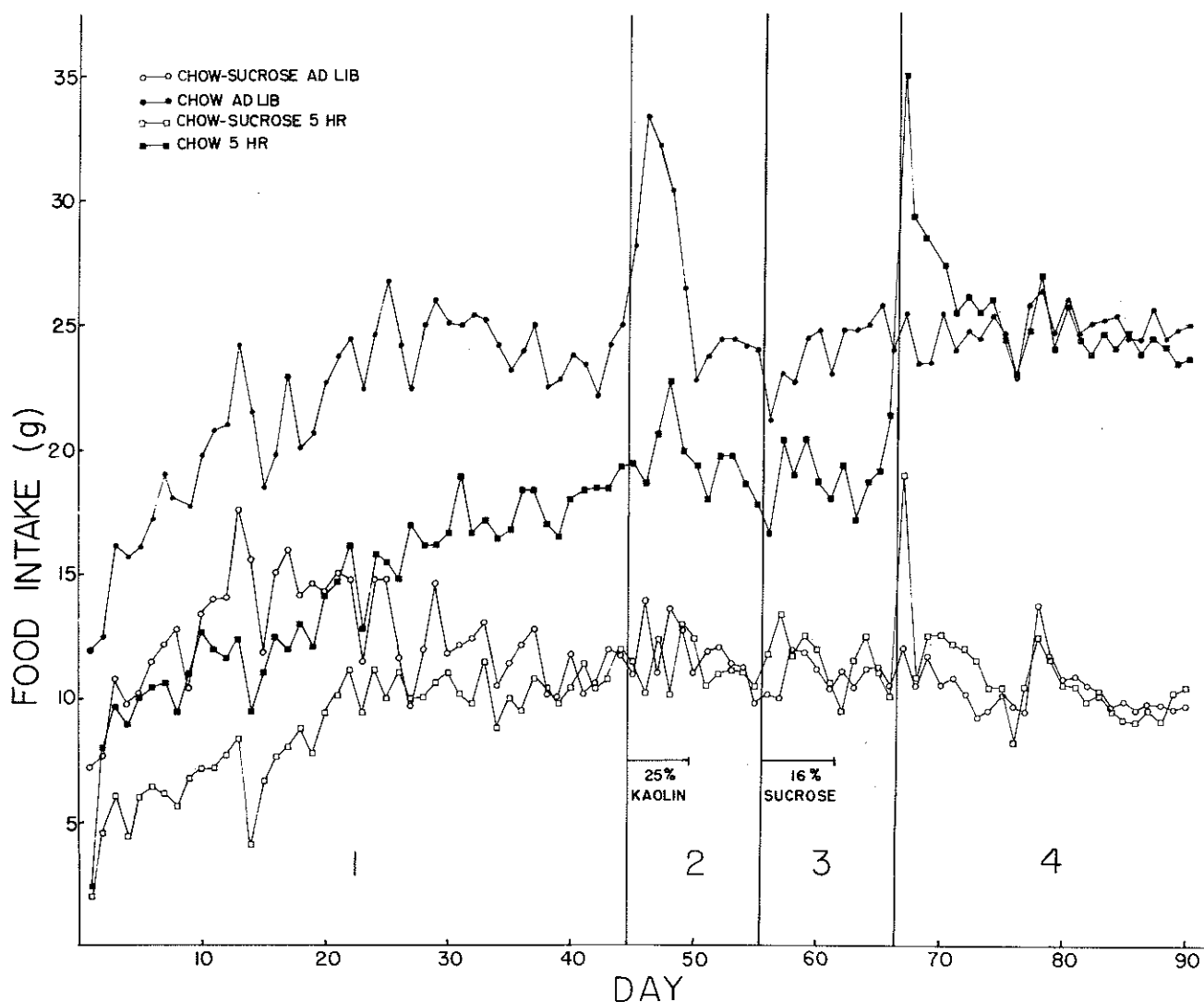
FIG. 3. Mean daily chow intake in rats fed a complete diet or a complete diet and a 32% sucrose solution for 5 hours or 24 hours each day.

ing manner. The 24 hour access groups consumed more chow than the 5 hour groups and the sucrose groups consumed less chow than the chow only groups. Chow intake increased over time for all groups except 24PS. In this group chow intake only increased for the first 20 days of phase 1 and then declined to the level of group 5 PS for the remainder of phase 1.

During phase 2 group 24P was the only group to show a significant increase in chow intake when this part of the diet was diluted with kaolin. Changing the concentration of sucrose from 32% to 16% did not influence chow intake for the two sucrose groups during phase 3.

During phase 4, when the restriction on food availability was removed, there was a substantial initial increase in chow intake. Chow intake declined within one day to the level of the appropriate control group for the group with access to sucrose. The decline to the control level of chow intake was considerably slower for the chow only group and took approximately eight days.

Figure 4 shows daily sucrose intake during the four phases of the experiment. During phase 1 the ad lib group consumed more sucrose than the restricted group. Both groups showed an increase in the absolute level of sucrose intake over time but the ad lib group showed a faster rate of increase. During phase 2, when the chow component of the diet was diluted, there was no change in sucrose intake for either group. When a 16% sucrose solution was substituted for the 32% solution both groups showed a prompt increase in consumption. In both cases this increase was not quite large enough to completely compensate for the dilution. As a result of this incomplete adjustment there was a 10 kcal decrease in the number of calories obtained from the carbohydrate solution. During phase 4 the formerly restricted animals showed a large increase in daily sucrose intake. For the first several days of phase 4 sucrose intake was higher in the formerly restricted animals but this value fell quickly to the control level.

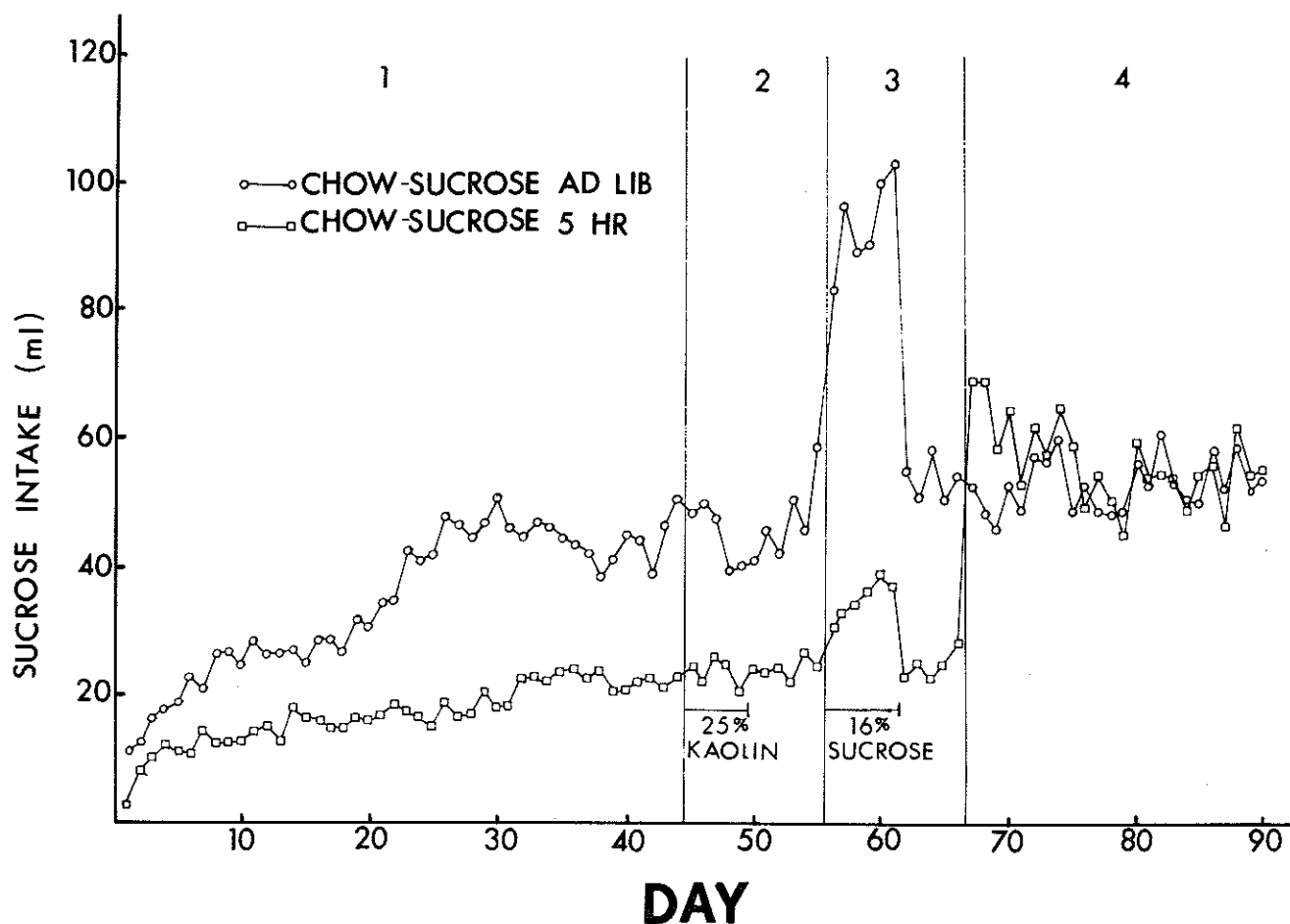Figure 5 examines relative sucrose intake by comparing

FIG. 4. Mean daily sucrose intake in rats offered a complete diet and a 32% sucrose solution for 5 hours or 24 hours each day.

the proportion of daily calories that were taken from the sucrose solutions in the two access conditions. This value was significantly higher in the ad lib group during phase 1. The proportion of calories taken from sucrose also increased from approximately 0.35 to 0.60 in this group during the first phase of this experiment. This value remained relatively constant at 0.40 for the 5 hr group. During phase 2, when the chow component was diluted, there was a small (8%) but statistically significant increase in relative sucrose intake. This increase was more pronounced in the restricted group. During phase 3 this proportion was lower when the 16% solution was offered. The lower value was largely due to the sharp decrease shown by the 5 hr group when the 16% solution was available. When the restriction on food availability was removed for the 5 hr group the proportion of calories taken from sucrose increased to the control level within one day.

One other feature of this figure stands out. The proportion of calories taken from sucrose shows a regular increase with age and changes in body size. The weanling takes about 35% of his daily calories from the sucrose solution whereas the 110 day old rat consumes almost 70% of his daily calories from the sapid solution.

Figure 6 emphasizes this point by plotting per cent protein intake over the course of the experiment. The analyses of

these data are not discussed because they are the inverse of the relative sucrose intake data. This figure clearly shows that weanling rats select about 15% of their diet as protein and this value decreases to about 8% at 110 days of age. This figure also shows that after approximately day 20 of phase 1 the restricted animals consume a higher fraction of their diet as protein than the ad lib animals. When food is provided ad lib these animals decrease their relative protein consumption to the control level. It should be noted that Fig. 6 shows per cent protein intake but functions of the same form would be obtained if fat or any of the vitamins or minerals present in the Purina chow were plotted.

DISCUSSION

The results of the present experiment reveal that access to a palatable carbohydrate solution can induce overeating in growing rats, but the rat's avidity for sucrose solutions does not lead to a pattern of dietary selection that compromises growth. Optimal selection and growth also occurred under deprivation conditions which would be expected to accentuate the rat's preference for carbohydrate solutions.

The overeating that was observed in the ad lib fed animals with access to sucrose is consistent with a number of other experiments conducted under similar conditions with both
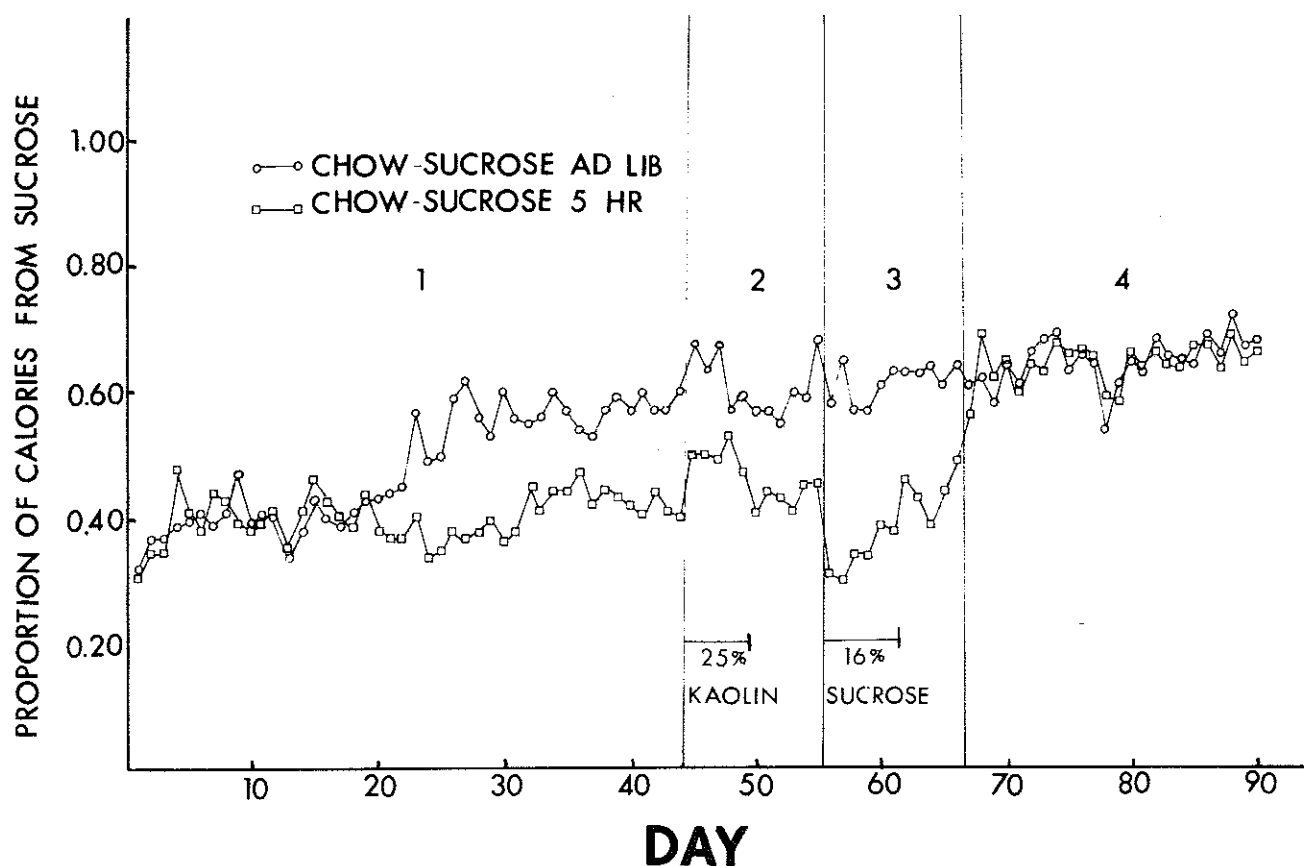
FIG. 5. Mean proportion of total caloric intake consumed from the sucrose solution in rats offered a complete diet and a 32% sucrose solution for 5 hours or 24 hours each day.

young rapidly growing rats [20,28] and adults [5, 9, 19, 21]. There are, however, several experiments which were conducted under very similar conditions that fail to find this small increase in daily energy intake when rats are offered a complete diet and a sapid, caloric solution [4, 7, 15, 17]. Part of this discrepancy may relate to relatively short periods of testing and the failure to include a chow fed control group in some of these experiments. Under these latter conditions the small but consistent elevation in caloric intake that was observed in the present experiment might be obscured. These considerations aside, there is at least one experiment that met these conditions and still failed to find overeating in rats offered a complete diet and a sucrose solution [15]. There are no obvious procedural or methodological differences to explain this discrepancy and at the moment these differential outcomes remain puzzling.

The present experiment also replicated the observation that young, rapidly growing rats with access to sucrose and a complete diet overeat but do not gain excess weight relative to a control group fed only the complete diet [20,28]. This uncoupling between excess caloric intake and body weight gain does not occur in the adult rat. When adult rats are offered a complete diet and a carbohydrate solution there is a discernible increase in body weight [5, 9, 19] that is accompanied by an increase in body fat content ([9], Hirsch and Powley, unpublished observations) and a proliferation of new fat cells [9]. The young rapidly growing rat with access

to sucrose also deposits excess fat and the Lee Index of obesity is elevated in these animals after only 25 days on the sucrose diet [20]. In the absence of a complete metabolic balance study on these animals it is reasonable to assume that the extra calories ingested are deposited as fat. The question of course remains as to why body weight is elevated in the adult rat offered this diet but not in the young, rapidly growing animal. One approach to this issue entails identifying when this transition occurs in order to isolate the underlying factors.

The present experiment was not completely successful in specifying the age at which excess caloric intake leads to an increase in body weight. At around 70 days of age the growth curves of the two ad lib fed groups began to separate but the magnitude of this effect was not large enough to produce a statistically reliable change in the rate of growth during the remaining 40 days of the experiment or in the final body weights of these two groups at 110 days of age. This pattern is strikingly similar to the growth curves presented by Muto and Miyahara [28] for animals fed either an 18% protein diet or an 18% protein diet and a 40% sucrose solution.

The age difference in the body weight response to excess caloric consumption assumes greater significance when it is appreciated that there is a striking human parallel to this situation. Although information on the incidence of human obesity is sketchy, somewhat inconsistent and difficult to compare across studies because of different definitions and
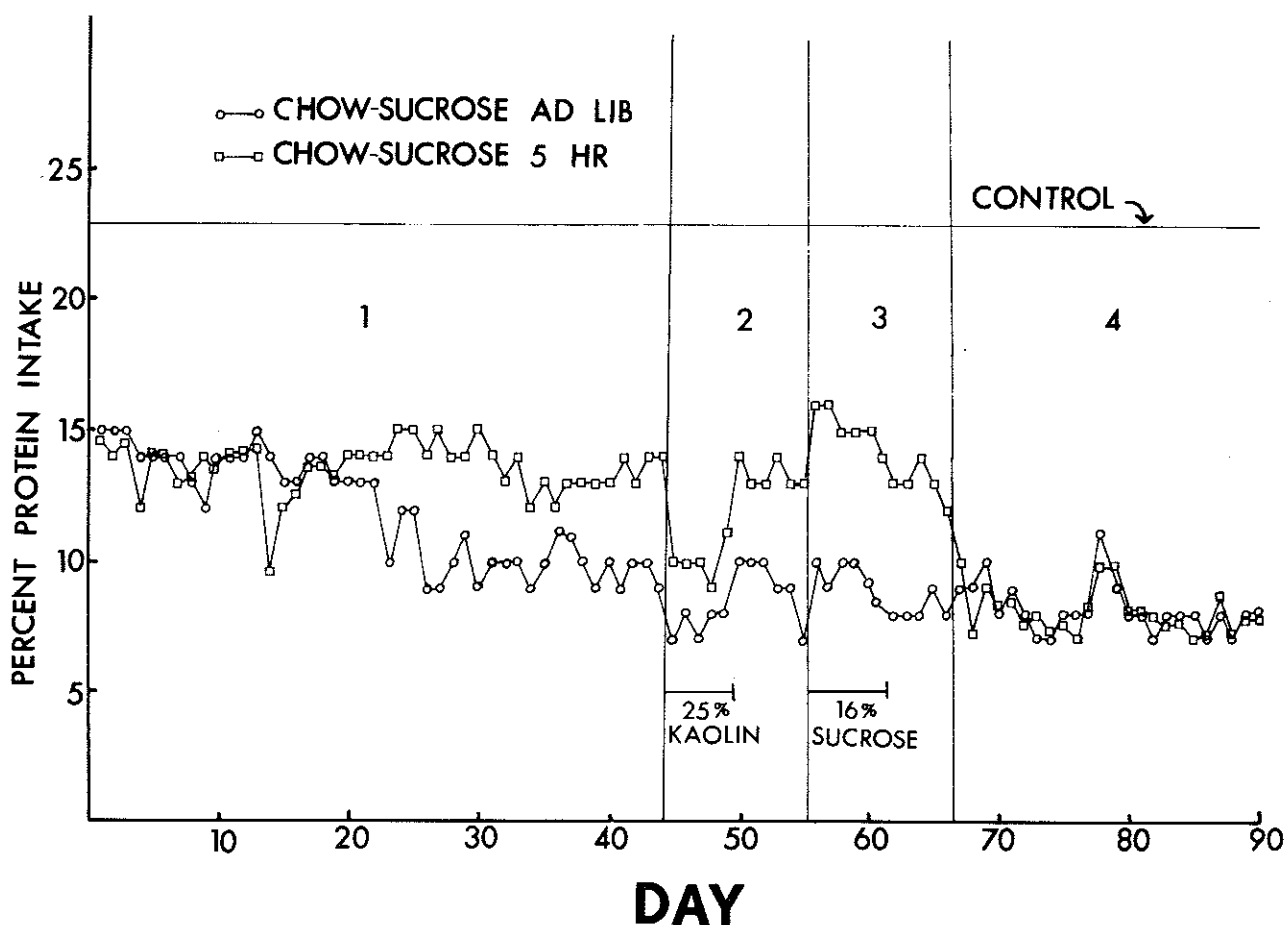
FIG. 6. Mean per cent protein intake in rats offered a complete diet and a 32% sucrose solution for 5 hours or 24 hours each day.

measures, the data that is available clearly reveals a trend towards an increase in the incidence of obesity with age. In children body weight exceeds the value expected from length in a surprising number of cases and values ranging from 16–35% have been reported for the incidence of childhood obesity [30,48]. During puberty the prevalence of obesity has been estimated at 10–15% of the population. In adults the age related trend becomes much clearer. Stunkard [45] has noted that between the ages of 20 and 50 the number of overweight individuals more than doubles. This tendency towards increasing weight with age is also apparent in the Metropolitan Life Insurance tables for both men and women [25]. Shank [43] has pointed out that increases in per cent body fat with age are even more pronounced than these weight changes. The apparent age dependence of weight increases in animal studies of carbohydrate-induced would seem to mirror these human trends and this procedure may provide a model for the experimental study of adult-onset obesity.

The pattern of results observed in the present experiment provides additional support for the view that the long term mechanisms which govern dietary selection also modulate the relative intakes of a complete diet and a sweet carbohydrate solution [7,8]. Weanling rats took approximately 35% of their daily energy intake as sucrose whereas adult rats took approximately 70% of their daily energy intake as sucrose. This change in relative sucrose intake with age is

entirely consistent with the well documented decline in the rat's protein requirement with age [14,24].

Relative sucrose intake was not solely dependent on age. The food restricted animals, who were smaller than the ad lib animals, showed a lower level of relative sucrose consumption. Sucrose and chow intakes appeared to be adjusted to meet the higher protein needs of these smaller animals. It should also be noted that this optimal pattern of selection occurred despite the fact that food deprivation would be expected to increase sucrose consumption in the restricted animals [6, 18, 47]. In one hour sessions this pattern of selection breaks down completely. When rats are offered a complete diet and a dilute sucrose solution [12,29] or glucose solution [40], the carbohydrate solution is consumed preferentially and the low caloric intakes that result lead to excessive weight loss and death. The one hour test session is obviously a demanding situation and may define the temporal boundaries of adequate selection with dilute solutions. Muto and Miyahara [28] have also observed poor selection when a low protein diet (9%) and a 40% sucrose solution were available to young growing rats.

The changes in food and solution intake that were observed during chow dilution and sucrose dilution are also consistent with a framework that emphasizes the controlling nature of the total nutritive economy of the animal. When the chow component of the diet was diluted complete caloric

compensation was not observed in any of the four groups. Despite the small reduction in total caloric intake the sucrose groups did not compromise dietary balance by consuming more of the carbohydrate solution. Under this condition neither caloric intake or dietary balance were perfrectly defended but the changes in intake were not large enough to produce observable effects on body weight during this short period. When the sucrose solution was diluted both groups showed a large increase in volume consumed. This increase was not quite sufficient to maintain relative sucrose intake at the level observed with the 32% solution.

The importance of dietary balance was also evident during the last phase of the experiment when the restricted groups were allowed free access to food. Both groups overate initially but within several days the sucrose group showed absolute and relative sucrose intakes that were indistinguishable from the group that had been raised with free access to chow and sucrose.

The preceding analysis is predicated on the assumption that the complete diet contains levels of the essential nutrients that are above the animal's minimal daily requirement. We have previously argued that this is the case for protein [8]. If the adequacy of the diet is judged by its ability to support optimal growth, it also appears that the other essential nutrients are available in surplus quantities in Purina chow. In both food availability conditions the animals with access to sucrose grew at precisely the same rate as the animals fed only Purina chow, although they ate considerably less of the chow and its associated nutrients. This line of reasoning suggests that the procedure used in the present experiment, or minor modifications of it, can be used to determine minimal daily requirements of the essential nutrients. At present these determinations are established in laborious balance experiments. According to this analysis the intake of a sweet carbohydrate solution should be a direct function of the level of the most limiting essential nutrient. In this regard it is interesting to note that the changes in sucrose intake with age in the present experiment appeared to be controlled by the growing animal's changing protein needs. The actual levels of protein intake that were observed are entirely commensurate with values obtained in balance experiments.

In summary the present data reveal that palatable carbohydrate solutions can lead to a small daily elevation in total caloric intake but they do not induce the rat to choose an unbalanced diet when a nutritionally adequate diet and a sweet solution are available for at least five hours. It appears that dietary balance has a higher priority than caloric constancy in the complex hierarchy of regulation and control in the feeding economy of the rate under the relatively permissive environmental conditions tested in this experiment.

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